Possible Behavioral Thermoregulation in *Tanarthrus salinus* and *T. inyo*

(Coleoptera: Anthicidae)

Randall M. Peterman[1]

Zoology Department, University of California, Davis, 95616

This paper describes several aspects of the biology of two desert-inhabiting species of anthicid beetles, *Tanarthrus* (*Tanarthropsis*) *inyo* Wickham and the rare *Tanarthrus salinus* LeConte. In particular, evidence will be presented to suggest that these insects have special adaptations for avoiding heat stress.

These beetles, which bear a superficial resemblance to ants, are, on average, 6 mm long and 2 mm wide, and 3.2 mm by 1 mm, the larger species being *Tanarthrus salinus*. The larger species is dark red-orange on the head, thorax, elytra and legs, with the abdomen being black, including the ventral and dorsal sides of its posterior tip which protrudes beyond the elytra by 1 mm. The hind wings are semi-transparent beige. *Tanarthrus inyo* is like *T. salinus* in coloration and general characteristics except that the elytra extend to the end of the abdomen and the rear half of the elytra are black. Both species are carnivorous scavengers, feeding on windblown material such as dead insects.

Methods

Observations were made in parts of August and September 1969 in a four square mile area in the middle of Carson Sink, near Fallon, Nevada. This area is a level, dry (but seasonally flooded) mud flat, lacking any form of plant life (except perhaps algae) and having only a small endemic animal population. There are few rocks and no standing water, and the soil surface is hard-packed. "Peeling" mud cakes in the usual sense are not found. On a macroscopic level then, the habitat appears to be relatively homogeneous. On the microhabitat level, however, the ground is more heterogeneous. Small cracks ranging from 1 to 5 mm in width are often found, and there are a few small (10 cm high) sand accumulations scattered throughout the area. The anthicids studied spend part of their time on the surface and part in these cracks, which offer them their only reprieve from direct sunlight.

Temperature data were gathered with a YSI telethermometer (50°

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[1] Present address: Institute of Animal Resource Ecology, University of British Columbia, Vancouver 8, B. C. Canada.

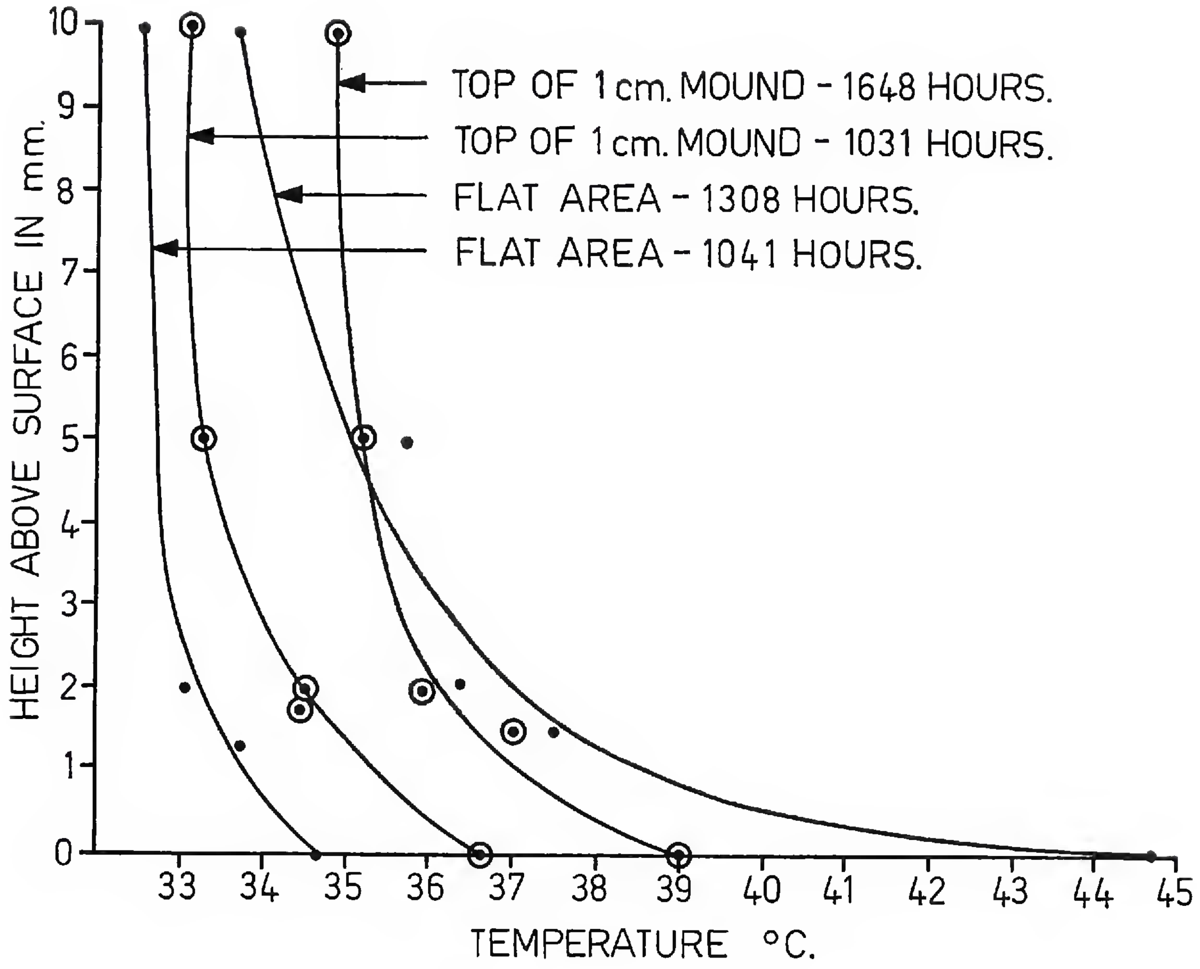

Fig. 1. Air temperature profiles on a typical day, 12 September 1969. The 1-cm mounds are where "thermoregulating" beetles perch.

C upper limit) and two number 403 thermistors. The small size (about 1 mm diameter) and short equalizing time (4 seconds) of these temperature probes permitted accurate temperature measurements of very small areas. Behavioral observations were mainly made with binoculars because beetles were so wary that usually no approach closer than two meters was possible.

Thermoregulatory Behavior

In the Sink winds of 0–5 mph normally prevail from the southwest and a thin superheated air layer less than 5 mm thick is produced just above the surface (Fig. 1). Living in such a warm environment, with daily summer surface temperatures ranging to above 50° C, both *Tanarthrus salinus* and *T. inyo* appear to have evolved two ways of avoiding heat stress. The first of these adaptations is morphological: the long, thin legs. The high surface-to-volume ratio of the legs in combination with their length minimizes the amount of heat which can be conducted through them from the ground to the body. In addition, the long legs, when stretched, lift the body up out of the superheated air layer into the wind turbulence, as noted by the rocking of the bodies back and forth with the wind gusts. This "stilting" behavior moves the main body axis up from 1.5 to 4.0 mm above the surface in *T. salinus* and from 0.8 to 1.4 mm in *T. inyo.* Such small increases in height accompany relatively large decreases in surrounding air temperatures (Fig. 1), perhaps large enough to make a significant difference in the body temperatures of these small beetles when they approach their upper temperature tolerances. Stilting has also been observed in scorpions (Alexander and Ewer, 1958) and tenebrionid beetles (Hamilton, 1971) and has been thought to be related to thermoregulation.

Another factor may be important in determining the body temperature of these very small animals: solar radiation (Pepper and Hastings, 1952). Here the second apparent adaptation comes into play—behavioral thermoregulation. The stilting described above is invariably accompanied by: (1) standing immobile on top of a small mound of dirt, (2) positioning the body approximately parallel with the sun's rays, with the head toward the sun and the anterior end of the body elevated slightly, and (3) for *Tanarthrus salinus* only, the beige hind wings extending out over the black tip of the abdomen (see Fig. 2). The first two characteristics tend to minimize heat gain by (a) moving into cooler surrounding air and (b) decreasing the angle of incidence of sunlight on the body. Such orientation with respect to incident solar radiation has been noted in grasshoppers, butterflies, and other beetles and has been shown to be an important factor regulating rates of heat gain (Clench, 1966; Edney, 1971; Heinrich, 1972; Kevin and Shorthouse, 1970; Pepper and Hastings, 1952; Watt, 1968). Other cases of behavior aiding the avoidance of heat stress have been reported for reptiles (e.g. Hamilton and Coetzee, 1969; Norris, 1953; Willard, 1966). The third characteristic of the observed anthicid behavior, extension of the light-colored hind wings, essentially replaces a black surface with a more reflective one, thereby decreasing the amount of heat absorbed by that region. Edney (1971), Hamilton (1973) and others have shown that light-colored insect surfaces keep underlying tissues significantly cooler than tissues under dark surfaces. Although these results have been obtained for insects larger than the present anthicids, it is probable that the wing-extending behavior of *Tanarthrus salinus* can make a small but significant difference in body temperature when the insects are nearing their upper lethal temperatures. *Tanarthrus inyo* does not exhibit wing-extending behavior because its elytra extend to the end of the abdomen.

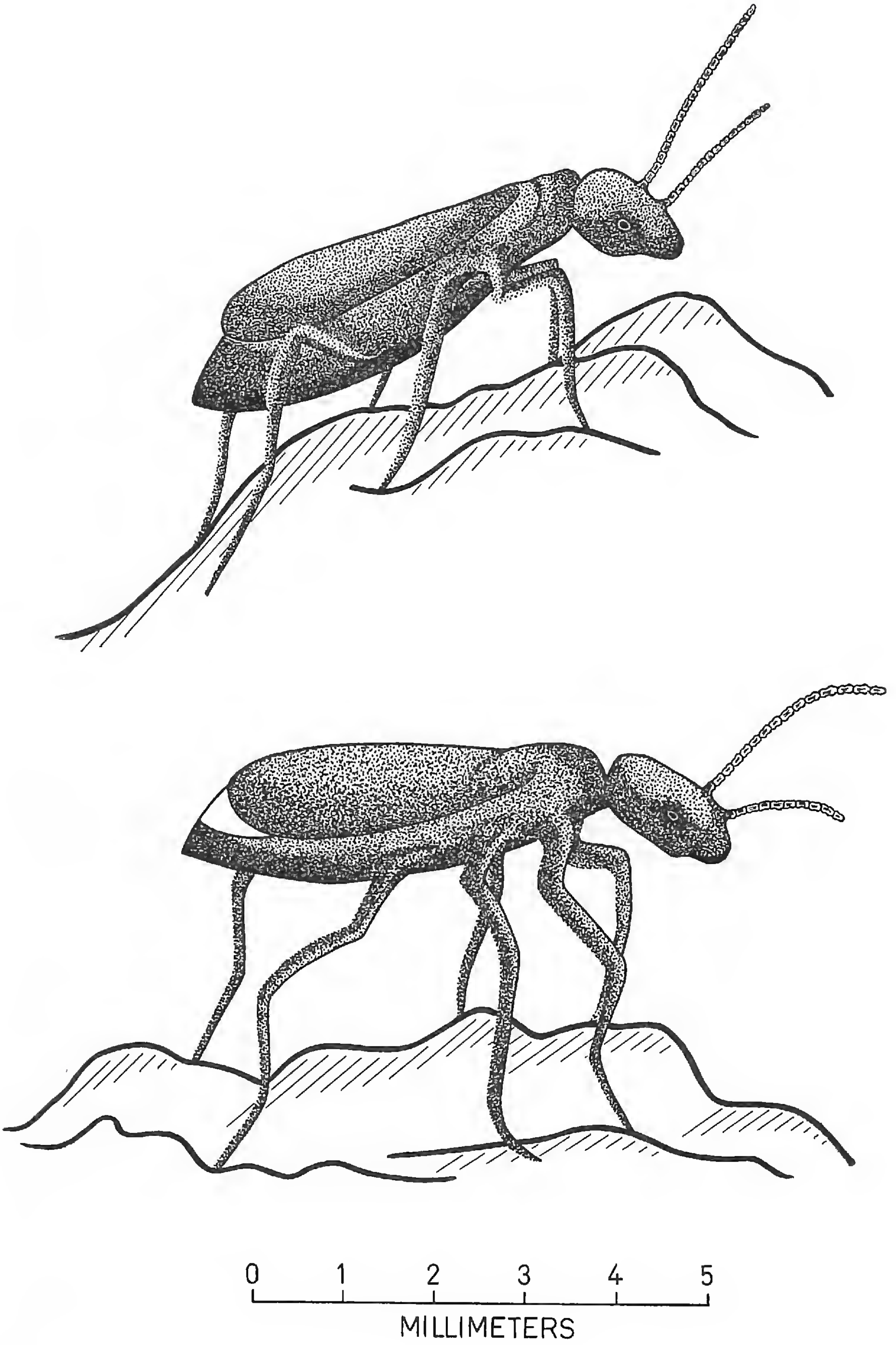

FIG. 2. *Tanarthrus salinus* in two stances, drawn from slides. Top figure is normal stance; bottom figure is "thermoregulatory" stance. Note the stretched legs and the hind wings out over the abdomen end.

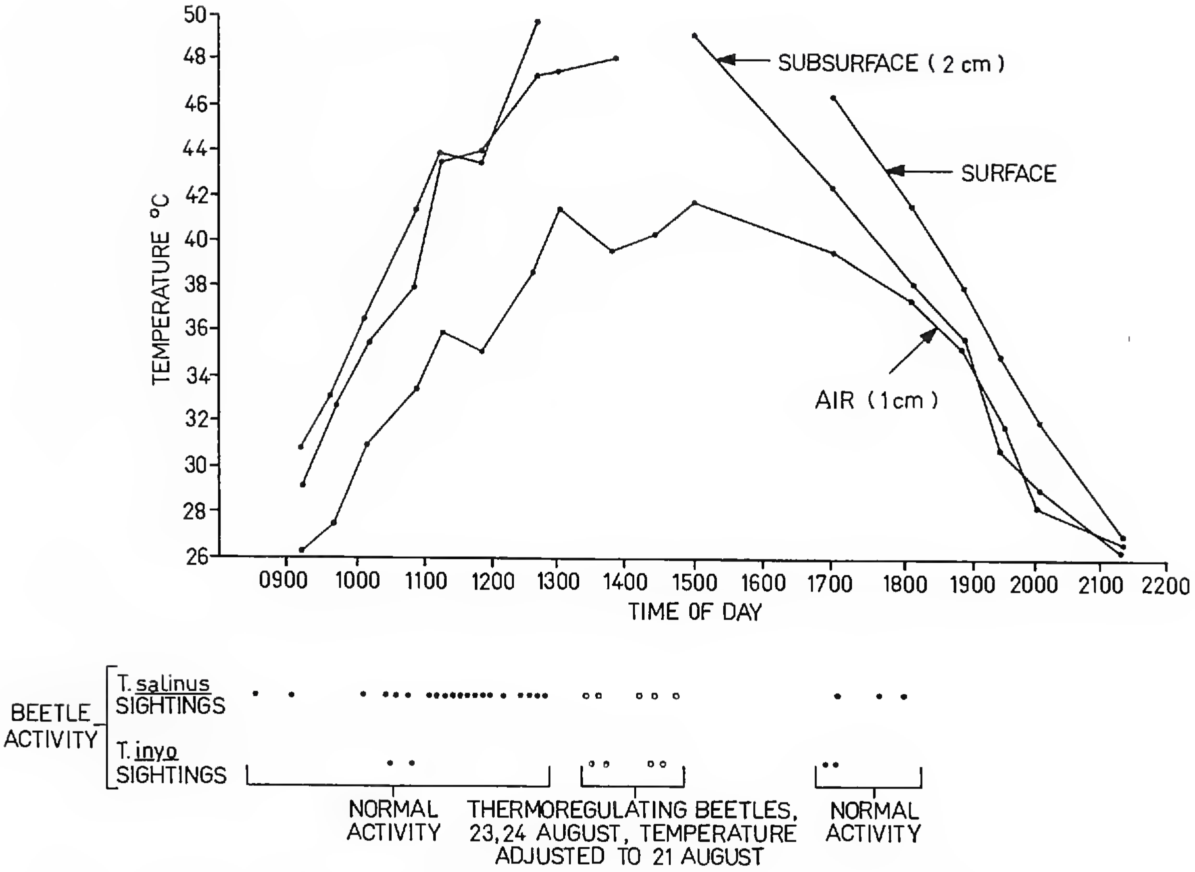

Fig. 3. Beetle activity periods and environmental temperatures on a typical day, 21 August 1969. In the beetle activity section at the bottom, one dot represents one sighting on that day at the indicated time.

Five observations support the hypothesis that the unusual behavior just described actually serves a thermoregulatory function (in the sense of avoiding a heat death, rather than maintaining a constant body temperature). The first is that normally the middle three or four hours of the day find no beetles above ground except in the shade of man-made objects. However, on the two hottest days experienced during the study, a total of 9 anthicids (5 of *T. salinus*) were seen on the surface in the midday period, and all were in the thermoregulatory postures (Fig. 3). The postures were not seen at any other time in the study for more than a few seconds. On the two hot days, these positions were maintained for up to 30 minutes. The beetles then disappeared when a duststorm struck the area on both days. Second, the beetles moved from this position only when the wind came up strongly, at which time they climbed down from their dirt perches to the shady side, only to climb back up when the wind died down, showing a definite favoring of this position. Third, just prior to the observed behaviors in the hot midday, literally dozens of both species flocked to the shade of the research facility (an open air shelter 3 m by 3 m), a phenomenon not seen previously in the study. Fourth, the hind wings of *T. salinus* were extended over their black-tipped abdomens only when accompanied by the other characteristics of the apparent thermoregulatory behavior, and vice versa. Fifth, when exhibiting this unusual behavior, both species were much less wary than normal. They could be approached by an observer to within a few centimeters, suggesting that they may have been in critical thermal states.

These five observations strongly imply that the two species have evolved behavioral adaptations for avoiding heat death. Normally, when the surface gets too hot, they go underground. However, on exceptionally warm days, the subsurface may be too hot (present data are inconclusive) and they might then have to resort to extreme means to cool off above the surface. Schmidt-Nielsen (1964), Edney (1967), Hadley (1970), Stower and Griffiths (1966), and Pepper and Hastings (1952) have pointed out for small desert insects that evaporative cooling can only contribute a minute amount to overall heat loss. Therefore, the only cooling mechanisms available to such insects are behavioral and morphological. Actual body temperature data are needed to critically test the hypothesis of behavioral thermoregulation, but present circumstantial evidence at least fails to negate the hypothesis.

ACKNOWLEDGMENTS

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Required six-month's notice is given of the possible use of plenary powers by the International Commission on Zoological Nomenclature in connection with the following names listed by case number.

(see *Bull. Zool. Nomencl.* 29, part 1, 1 May 1972)

1944. Suppression of *Lyda inanis* Klug, 1808 (Insecta, Hymenoptera)
1979. Type-species for *Uloma* Dejean, 1821 (Insecta, Coleoptera)

(see *Bull. Zool. Nomencl.* 29, part 3, 30 November 1972)

1989. Type-species for *Anobium* Fabricius, 1775, *Grynobius* Thomson, 1859, and *Priobium* Motschulsky, 1845 (Insecta, Coleoptera)
1994. Type-species for *Dicyrtoma* Bourlet, 1842, and *Dicyrtomina* Börner, 1903; suppression of *Podura minuta* O. Fabricius, 1783, and *Papirius cursor* Lubbock, 1862; validation of *Papirius fuscus* Lubbock, 1873 (Insecta, Collembola)
1998. Type-species for *Deuterosminthurus* Börner, 1901 (Insecta, Collembola)
1999. Type-species for *Eusminthurus* Börner, 1900 (Insecta, Collembola)

(see *Bull. Zool. Nomencl.* 29, part 4, 29 December 1972)

1979. Type-species for *Phaleria* Latreille, 1802 (Insecta, Coleoptera)
1948. Validation of RIODINIDAE Grote, 1895 (Insecta, Lepidoptera)
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